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ZYGOBOTHRIA NIDICOLA, AN IMPORTANT PARASITE OF THE BROWN-TAIL MOTH.

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INTRODUCTION.

One of the most effective factors in the control of the brown-tail moth (*Euproctis chrysorrhoea L.*) in the United States is the introduced tachinid fly *Zygobothria nidicola* Townsend. Strangely enough this European parasite had not been described at the time it was first obtained in this country. The first adults were reared at the Gipsy Moth Laboratory, then located at North Saugus, Mass., in the summer of 1906, from brown-tail moth caterpillars that had been received from Europe during the preceding winter. The specimens were referred to Mr. C. H. T. Townsend, of the Bureau of Entomology, United States Department of Agriculture, for identification. After some correspondence with European authorities, to whom also specimens were submitted for examination, Mr. Townsend concluded that the species was new, and subsequently described it under the name *Zygobothria nidicola.*[2]

Much difficulty was experienced in rearing adults of the parasite for colonization from imported brown-tail moth larvæ. This was due to the great mortality among the caterpillars, particularly from

[1] Special acknowledgments are due Mr. A. F. Burgess, in charge of Gipsy Moth and Brown-tail Moth Investigations, for helpful criticism of this bulletin, and Messrs. S. S. Crossman and R. T. Webber, of the Gipsy Moth Laboratory, Melrose Highlands, Mass., for many suggestions during the prosecution of the work.

[2] Townsend, Charles H. T. The taxonomy of the muscoidean flies, including descriptions of new genera and species. *In* Smithsonian Miscellaneous Collections, v. 51, p. 99–101. 1908.

disease, before the parasites completed their development. Despite the discouraging results of the breeding work, however, *Z. nidicola* became established, and by 1910 had definitely taken its place in our fauna. The trying experiences of the laboratory force, in their attempts to establish this parasite, are interestingly recounted by Howard and Fiske.[3]

DISTRIBUTION IN THE UNITED STATES.

Because it evidently has no hosts other than the brown-tail moth the parasite must necessarily remain within the area over which this insect occurs; but within these limits it appears to be widely distributed, although it is relatively less abundant in the sections where very low temperatures are reached during the winter. It has been recovered from Rhode Island to northeastern Maine—very abundantly in the former region, sparingly in the latter. This wide dissemination, within some seven or eight years, is very largely the result of natural spread, since there has been little artificial colonization of this species.

LIFE CYCLE OF THE BROWN-TAIL MOTH.

Before taking up in detail the biology of the parasite it will be well to review briefly the life cycle of its host. During July the female brown-tail moth deposits her eggs on the underside of a leaf of one of the favored food plants—apple, pear, oak, or wild cherry. Usually the terminal leaves of the uppermost shoots of the tree are selected for oviposition. The eggs hatch in about three weeks and the small caterpillars feed on the epidermis of the leaves, preferring the terminal ones, which they gradually tie together with a large amount of silk. This process is slow, but ultimately a firm, tough web, about 3 or 4 inches long, is formed. By this time the majority of the slowly growing larvæ are in the third stage and are ready for hibernation. In the spring feeding begins as soon as the buds open, and continues until the middle of June, when cocoons are formed and pupation occurs. Moths issue during the first half of July, and, after a few days, lay their eggs. There is only one generation annually.

LIFE HISTORY AND BIOLOGY OF THE PARASITE.

EMERGENCE AND LONGEVITY OF THE ADULTS.

Adults of *Z. nidicola* appear during the latter half of July. They are very sturdy flies (Fig. 1) and endure unfavorable conditions well, normally living for a period of at least several weeks. Some

[3] Howard, L. O., and Fiske, W. F. The importation into the United States of the parasites of the gipsy moth and the brown-tail moth. U. S. Dept. Agr., Bur. Ent. Bul. 91, p. 289–295. 1911.

specific data with regard to the length of life were obtained from laboratory experiments in which various types of cages were used. These consisted of: (1) Plain glass cylinders, measuring 50 by 200 mm., closed at one end; (2) ordinary shell vials, 22 by 100 mm.; and (3) a wooden cage, which had been successfully used by Mr. J. J. Culver in his life-history studies upon *Compsilura concinnata* Meigen, a tachinid parasite of both the brown-tail moth and the gipsy moth.

The glass cylinders were rather satisfactory for two to five flies each, when a bit of crunched crêpe paper was placed inside to afford the flies a good footing, but it was necessary to change the cylinders

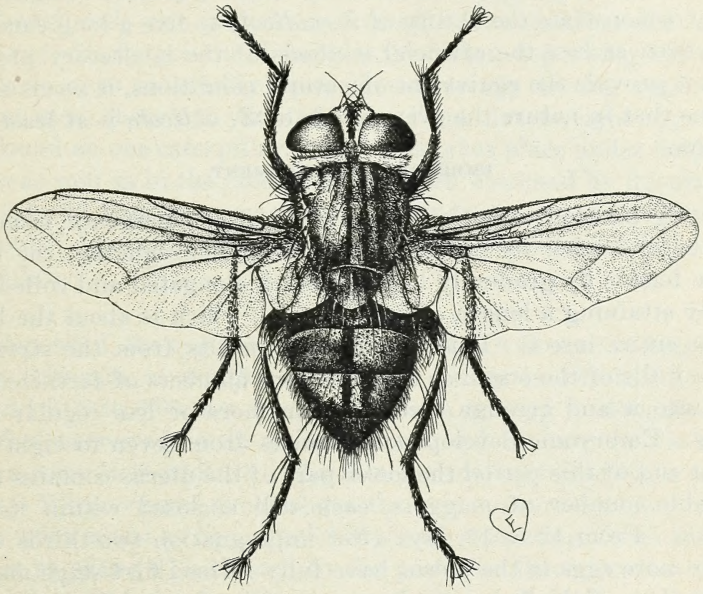

FIG. 1.—Adult male of *Zygobothria nidicola*.

every few days because they quickly became dirty and sticky, and this involved a good deal of work. This objection applied to the shell vials as well, which in addition were found to be too small even for individual flies. The wooden cage was by far the most satisfactory. It measures about 12 inches square and 4 inches high, and is fitted with a cloth bottom to facilitate cleaning after each experiment; the top is a piece of window glass of the proper size. One-inch holes bored in the sides of the box and covered with fine wire gauze insure good ventilation. Another opening of the same size is fitted with a cork and is used for introducing the flies. Feeding is facilitated by the use of a larger opening, about 2 inches in diameter, which can be closed with a wooden stopper. After the flies were placed in this cage they were left entirely alone save for the feeding, which

was done on alternate days. This process merely involved slipping a narrow strip of blotting paper, which had been soaked in a mixture of honey and water, into the cage, and removing the old strip which had been placed there two days before.

Only a small proportion of the flies confined in the glass cylinders or shell vials lived from 25 to 28 days, and then only upon receiving particularly good care; those in the wooden cages which were given comparatively little attention lived five weeks and more. Two males and one female, which were confined in one of these wooden cages, were apparently in as good condition at the end of a 40-day period, when the experiment was discontinued, as when first placed in the box; several larger lots did about as well. The data obtained certainly demonstrate the ability of *Z. nidicola* to live a long time; and since even at best the artificial methods of the laboratory probably can not provide the equivalent of natural conditions, it seems safe to assume that in nature the average life of *Z. nidicola* is at least 25 to 30 days.

EMBRYONIC DEVELOPMENT.

Mating takes place within a few hours after emergence, sometimes even before either fly has fed. Following impregnation the uterus of the female fly gradually becomes much elongated and coiled, ultimately attaining a length of 7.5 to 8 mm., which is about the length of the entire insect. This enlargement results from the stretching of the walls of the organ as the enormous numbers of fertilized eggs pass into it and arrange themselves in more or less regular spiral layers. Embryonic development requires from seven to eight days. At the end of this period the lower part of the uterus contains a considerable number of maggots, each still enclosed within its egg-chorion. From 12 to 16 days after impregnation two-thirds of the 600 or more eggs in the uterus have fully formed first-stage maggots within them, if the fly has not been ovipositing as rapidly as they have developed.

OVIPOSITION.

The female fly prefers as its victims brown-tail moth caterpillars that are from several days to two weeks old, but even those just out of the egg are often successfully parasitized. Most of the oviposition by this species takes place during the first three weeks of August, in normal seasons.

Oviposition was readily obtained in the laboratory by confining a fertilized female fly in a shell vial with a few brown-tail moth larvæ that had been placed upon a small piece of cherry leaf. Having found the caterpillars, the parasite manifested much interest, passing slowly from one larva to another and inspecting each minutely. Then, with her face but a few millimeters from one of

the caterpillars, she slowly and deliberately pushed her abdomen downward and forward until the ovipositor plates were even with her face. With a quick movement the ovipositor was then pushed beneath the larva, and an egg with a first-stage maggot within it was deposited. The egg is almost invariably placed on the venter of the host, and usually occupies a transverse position between two pairs of true legs, or, less frequently, between two pairs of prolegs. Occasionally an egg is placed on the dorsum by accident, but in such cases the parasitic maggot is unable to enter its host—at least this was true of instances under observation in the laboratory. The explanation probably is to be found in the thicker skin of the dorsum, which is not so easily pierced by the small maggot.

Although only one parasite can complete its development in one host larva, the fly uses no discrimination when depositing her eggs; she places eggs as readily upon larvæ already having eggs upon them as upon those not yet attacked. From five to eight eggs have been found on one caterpillar. That this takes place under field conditions as well as in the laboratory has been disclosed by dissections; from 6 to 10 first-stage maggots of the parasite have been not uncommonly dissected from single field-collected brown-tail moth caterpillars.

EGG.

As deposited, the egg measures from 0.42 to 0.45 mm. in length by 0.11 to 0.12 mm. in width; the maggot within is 0.33 to 0.35 mm. long and 0.08 to 0.09 mm. broad. In form the egg is elongate-oval, somewhat narrowed at the posterior end, and concave on the lower side; in color it is whitish. The thin and delicate chorion is transparent. When viewed from above the egg appears opaque; this is due to what seems to be a special layer of protecting tissue just inside the chorion; it is limited to the posterior three-fourths of the egg, and occurs only above the maggot. It is peculiarly reticulated, being marked off into very slender hexagons, the outermost of which are incomplete. Its position suggests its function to be that of affording protection to the young maggot before the latter succeeds in boring into its host.

ENTRANCE OF MAGGOT INTO HOST.

Having been placed upon its host the parasitic maggot begins to cut through the thin egg chorion that confines it, and as soon as this is done it bores into the caterpillar. The posterior end of the parasite remains inside the eggshell until the opening into the host has been made; when this has been accomplished it requires but a fraction of a second for the maggot to pull its whole body into the caterpillar. In one case under observation the entire process of cutting through the egg chorion and the host skin and entering the

brown-tail moth caterpillar was completed within 10 minutes after the egg had been deposited. From many observations it appears that normally 20 to 30 minutes elapse between oviposition and the entrance of the parasitic larva into its host. Often the caterpillar makes vigorous attempts to destroy the maggot before the latter has made its way inside, and occasionally these efforts are successful, particularly if the egg of the parasite was deposited near the posterior end of the host. In this case the brown-tail moth larva, by doubling its body, can reach the parasite and crush it with its mandibles.

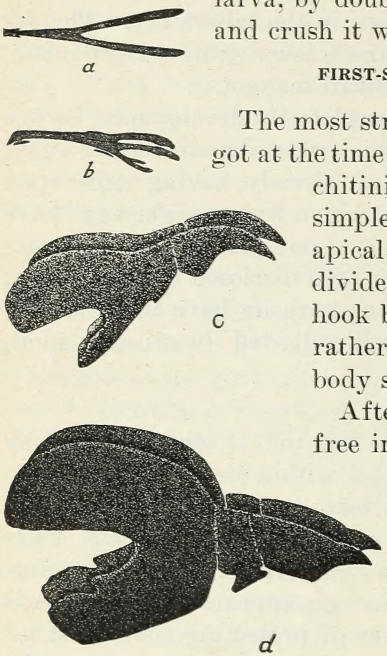

FIG. 2.—*Zygobothria nidicola: a*, Mouth hook of first-stage maggot, dorsal aspect; *b*, mouth hook of first-stage maggot, lateral aspect; *c*, mouth hook of second-stage maggot; *d*, mouth hook of third-stage maggot.

FIRST-STAGE MAGGOT OF THE PARASITE.

The most striking thing about the parasitic maggot at the time it enters the caterpillar is the strongly chitinized mouth hook (Fig. 2, *a*, *b*). It is simple in this stage, consisting of a single apical tooth and comparatively narrow, divided, posterior plates, the entire mouth hook being one solid structure. A pair of rather indistinct spiracles open on the last body segment.

After entering its host the parasite lives free in the body cavity for about 10 to 14 days and feeds on the fat body of the slowly developing caterpillar. Then it enters the œsophagus and remains here throughout its hibernation period of about nine months. It may lie longitudinally disposed or it may lie obliquely; apparently no particular part of the œsophagus is preferred, but usually the head of the parasite is directed toward the anterior end of its host. From dissections it appears that the maggot lies in a cyst against the inner wall of the intestine. Here, of course, it does not feed at all.

Rather severe competition is encountered from two hymenopterous parasites, *Apanteles lacteicolor* Viereck and *Meteorus versicolor* Wesmael, which also hibernate in the small brown-tail moth caterpillars. The presence of either of these parasites in the same host with Zygobothria produces the death of the latter. The exact nature of this peculiar influence exerted by the hymenopterous parasites upon the dipterous larva has not yet been demonstrated. Death

may perhaps result from a direct secretion of the hymenopterous species, or it may follow some special reaction on the part of the host; at no time has evidence of active combat been found.

In the spring the brown-tail moth larvæ that have hibernated begin feeding as soon as the buds open, but the Zygobothria maggots, in their cysts in the œsophagus, remain inactive for several weeks longer. It is not until late May and early June, when the host larvæ have molted into the last stage, that the parasite leaves its cyst in the fore-intestine and again enters the body cavity of the caterpillar to feed. Invariably it works its way at once to the posterior end of the host. After three or four days it is found to have established communication with the outside air through an opening in the integument of the brown-tail moth larva. From this minute, more or less circular opening there proceeds a rapid growth of the integument into the body cavity. This ingrowth takes the form of a funnel, within which the parasite lies, its posterior end directed toward the small opening, its anterior end free in the fat and fluids of its host. Thus the parasite has procured for itself an independent air supply. On the outside of the integumental funnel layers of soft tissue, evidently consisting of hypodermal cells, leucocytes, and compressed fat-cells of the caterpillar, are gradually laid down, one upon another, until a thick, fleshy wall has been formed about the funnel.

The manner in which the opening through the body wall of the brown-tail moth larva is effected was not observed. Possibly it results from irritation by the spines at the caudal end of the parasitic maggot.

SECOND-STAGE MAGGOT OF THE PARASITE.

Very soon after becoming established in the posterior end of its host, and in the integumental funnel, the parasite molts into the second stage. The first-stage skin is pushed back upon the funnel where it is readily detected by the presence of the mouth hook. The second-stage maggot is distinguished from that of the first stage by its larger size, the much heavier mouth hook, and the presence of a pair of anterior spiracles, often difficult to locate, situated between the second and third body segments. Instead of the single apical tooth of the first stage the mouth hook now has two teeth, the pharyngeal skeleton having divided longitudinally over its anterior half; furthermore, there is now an indistinct transverse joint near the middle of this anterior portion. The posterior plates of the mouth hook are much stouter than in the first stage.

Throughout this instar, which requires from 8 to 12 days, the maggot remains in the integumental funnel. It grows rapidly during this period so that it measures about 4 mm. in length when ready to molt into the third and last larval stage. By this time the host has spun its cocoon.

THIRD-STAGE MAGGOT OF THE PARASITE.

When the second-stage skin is molted it is pushed back upon the funnel, as was that of the first stage; the mouth hooks of the two instars at this time are easily seen on the mass of yellowish tissue that surrounds the chitinous funnel itself. The particular points of difference between the second and third stage maggots are the larger size of the latter and its much heavier mouth hook. The mouth hook is divided longitudinally as in the second stage, but there are now two joints in the anterior part of the skeleton, one near the middle, corresponding to the single joint of the second stage, and another near the base of the very broad posterior plates. The anterior spiracles, opening between the second and third body segments, are much more distinct than in the second instar.

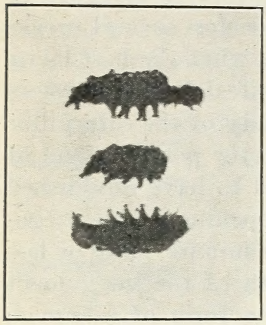

FIG. 3.—Brown-tail moth caterpillars containing puparia of *Zygobothria nidicola.*

This stage is the shortest of the three, requiring only four or five days. The host larva is killed just before the end of this period, with the destruction of its vital organs, and the parasite forms its puparium in the integumental funnel inside the host.

The puparium is about 8 mm. long and is dark brownish red in color; the posterior end is a little depressed, and the two anal stigmata (Fig. 4) within the depression are slightly elevated. Dead caterpillars that contain puparia of *Z. nidicola* (Fig. 3) are easily detected; they are greatly shortened, being scarcely longer than the puparia within, and are slightly inflated.

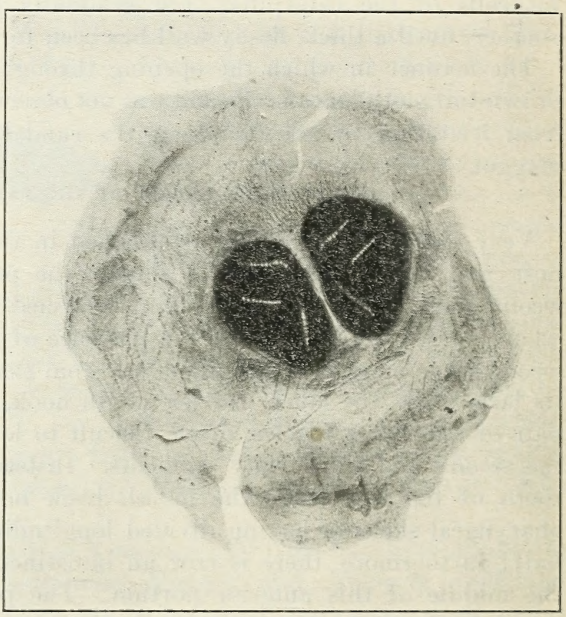

FIG. 4.—Anal stigmata of puparium of *Zygobothria nidicola.*

The period spent in the puparium averages from 25 to 30 days, after which the flies appear, some 8 to 16 days prior to the hatching

of the eggs of the brown-tail moth. This is just time enough to insure fertilization and development of the ova. Thus the life cycle of *Zygobothria nidicola* fits perfectly into that of its host.

ECONOMIC IMPORTANCE OF THE PARASITE.

Although *Zygobothria nidicola* has only one generation a year, and is handicapped by its absolute dependence upon the brown-tail moth, it has become a common species in New England. This means that it is of very great importance in the natural control of the brown-tail moth. Especially in the southern part of the infested area has the parasite proved remarkably effective, despite the fact that it is always the loser when in competition with *Apanteles lacteicolor* or *Meteorus versicolor*. In dissections of thousands of hibernating brown-tail moth caterpillars from all sections of New England it has been common to find from 20 to 30 per cent parasitism by Zygobothria.

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